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Rain Forest and Xeric Flora Refuges in French Guiana

Jean-Jacques de Granville

ABSTRACT After a short description of the natural environment in French Guiana and of the chronology of the recent climatic variations, the probable evolution of the flora and vegetation due to these fluctuations is analyzed in terms of climatic, topographic, and mainly pedologic and floristic data. Thus the approximate limits of a rain forest refuge in French Guiana during the great arid phase of the late Pleistocene are postulated. On the other hand, the present-day situation, corresponding to the end of a wet period, supports the evidence of isolated refuges with a xeric, herbaceous flora (coastal savannas, outcrops, forest canopy).

SITUATED BETWEEN 2° and 6° latitude North on the Precambrian base of the "Guayanian shield," French Guiana covers an area of approximately 90,000 km^2 (fig. 12.1).

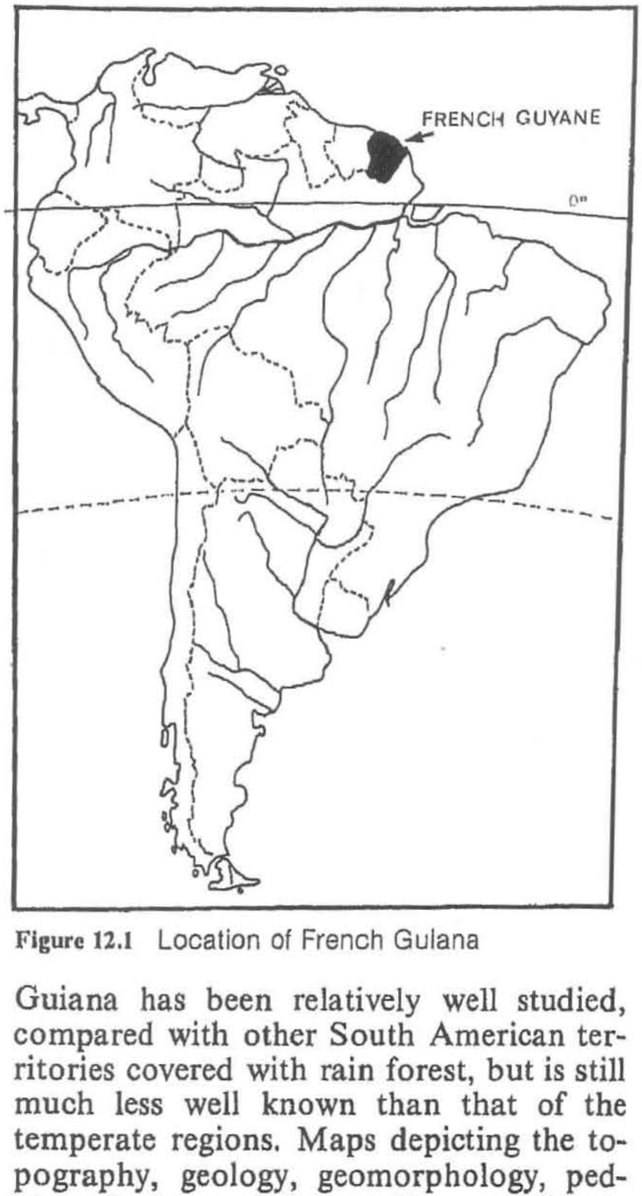


Figure 12.1 Location of French Guiana

The natural environment of French Guiana has been relatively well studied, compared with other South American territories covered with rain forest, but is still much less well known than that of the temperate regions. Maps depicting the topography, geology, geomorphology, pedology, hydrography, vegetation, and climate (*Atlas de la Guyane* 1979) have been drawn up. The human impact on the natural ecosystems is negligible, due to the very low population density which is essentially urban (50,000 population, of which 30,000 is in Cayenne) and to the lack of industry, agriculture, and roads to the interior.

Only on the very narrow coastal zone of French Guiana (fig. 12.2) where the Qua-

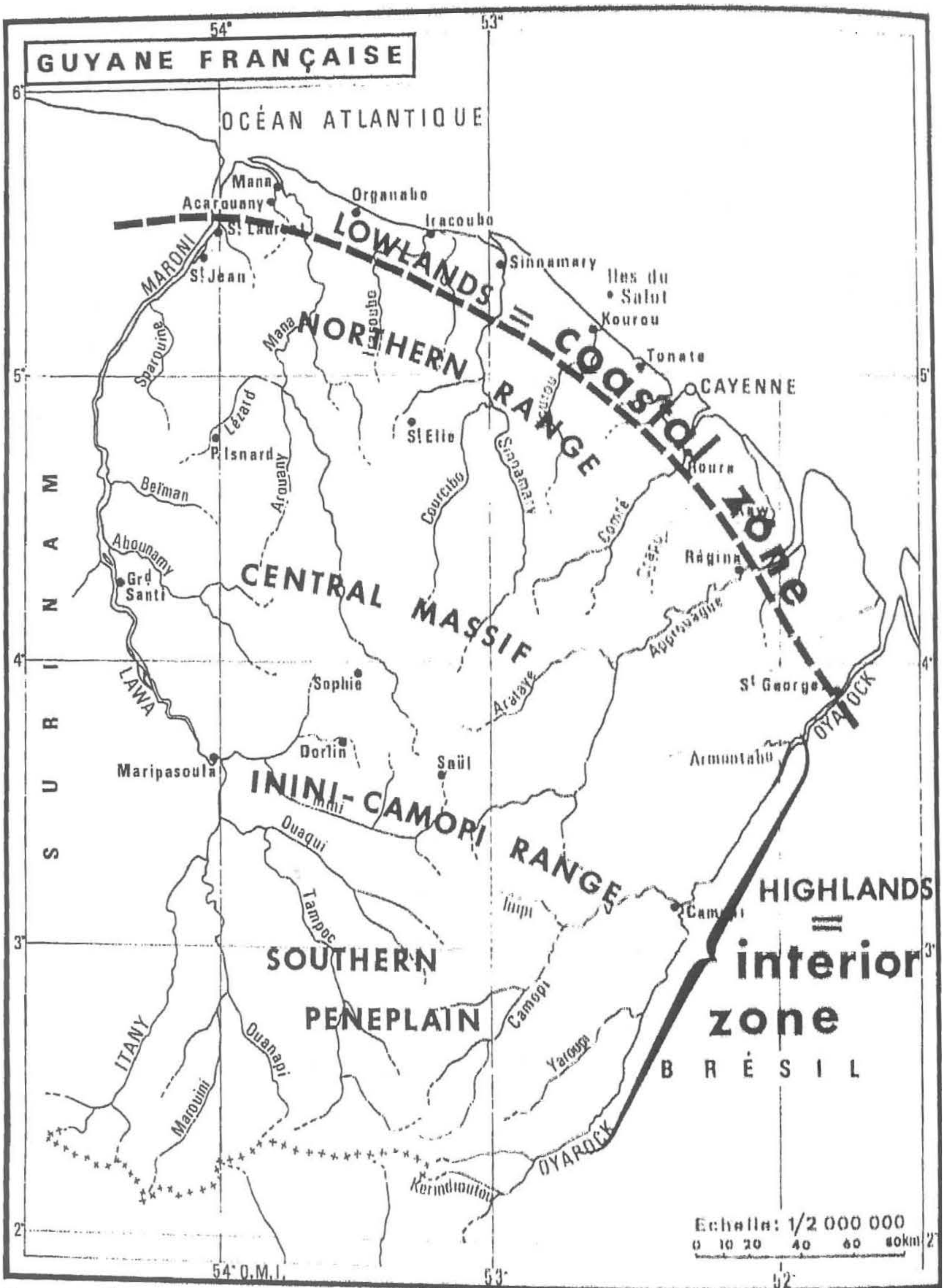


Figure 12.2 The principal geographic regions of French Guiana

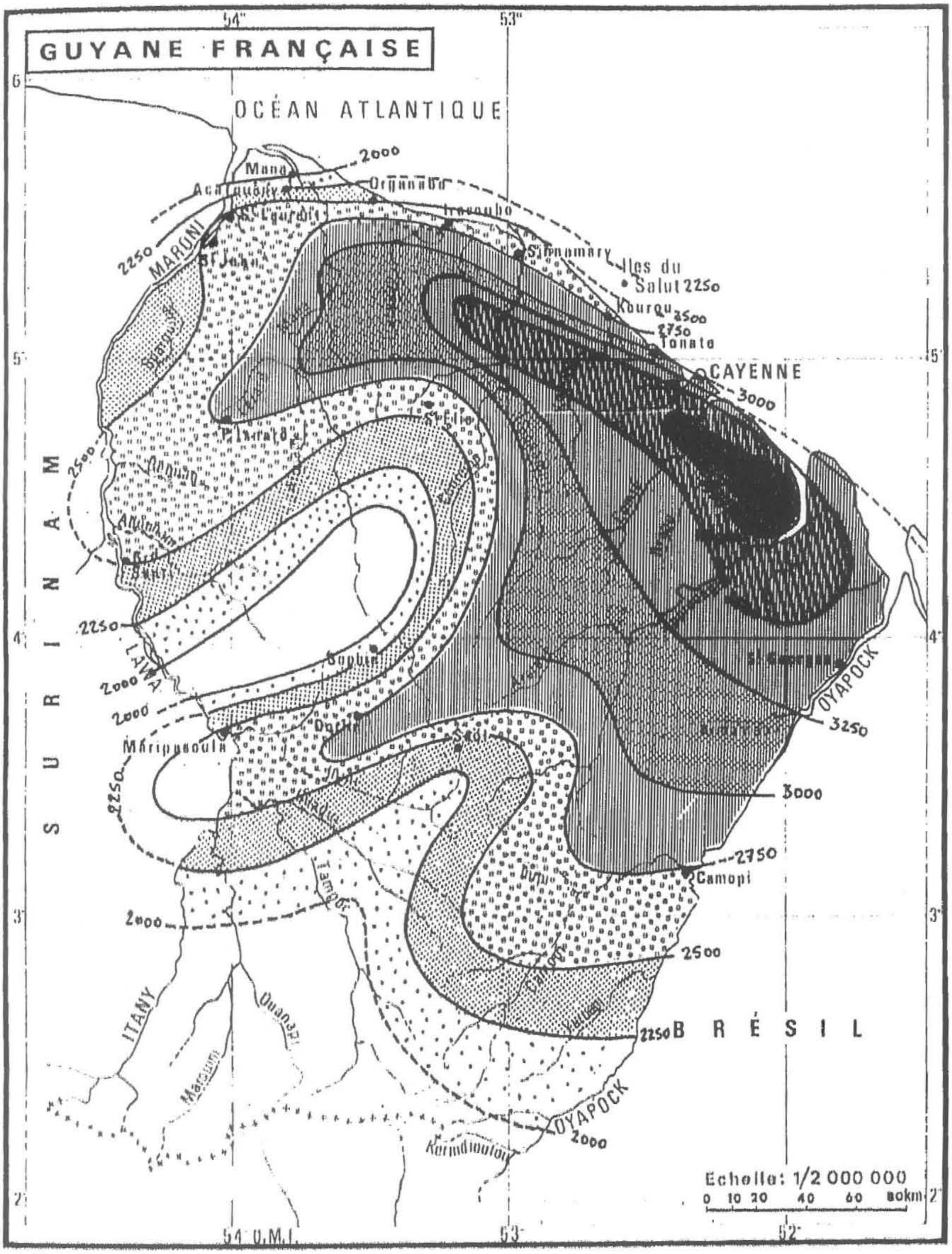


Figure 12.3 Rainfall map of French Guiana

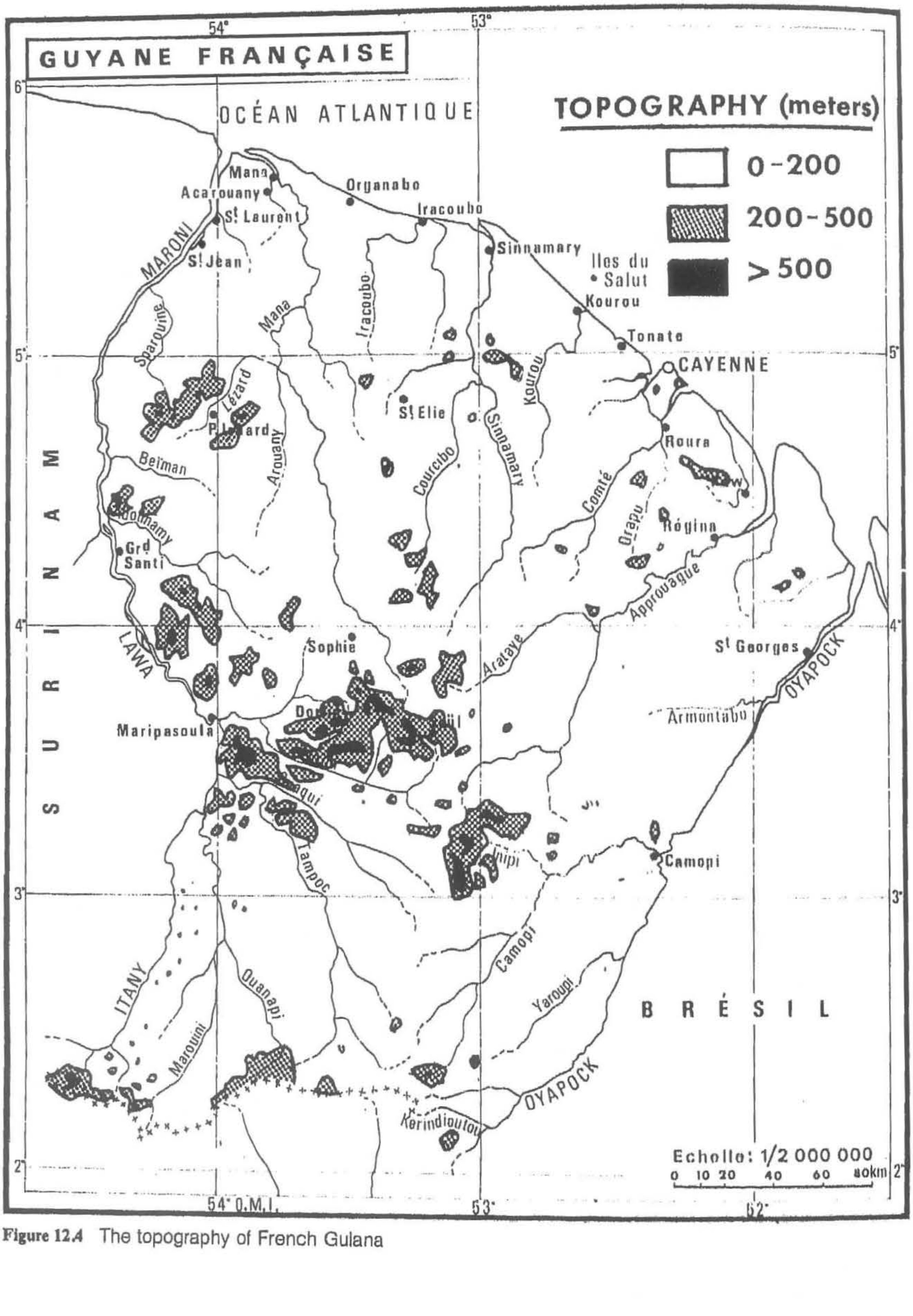


Figure 12.4 The topography of French Guiana

ternary marine sediments overlie the Precambrian base, does a nonforested vegetation exist. This is made up of mangrove (0.6% area of French Guiana), savanna and coastal swamps (1.7%).

The interior zone (fig. 12.2), which almost completely covers French Guiana, corresponds to the position of the Precambrian base. Today this zone is covered with dense equatorial rain forest which occupies more than 97 percent of the total area of French Guiana. Its physiognomy is in general fairly uniform in spite of an unequal distribution of the rainfall which varies according to the region from less than 2,000 mm to more than 4,000 mm/year (fig. 12.3). It is an evergreen forest which grows on ferralitic soils on a sloped but rarely steeply inclined relief, and where the multiconvex pattern, on granite, called "demi-oranges" is the most common.

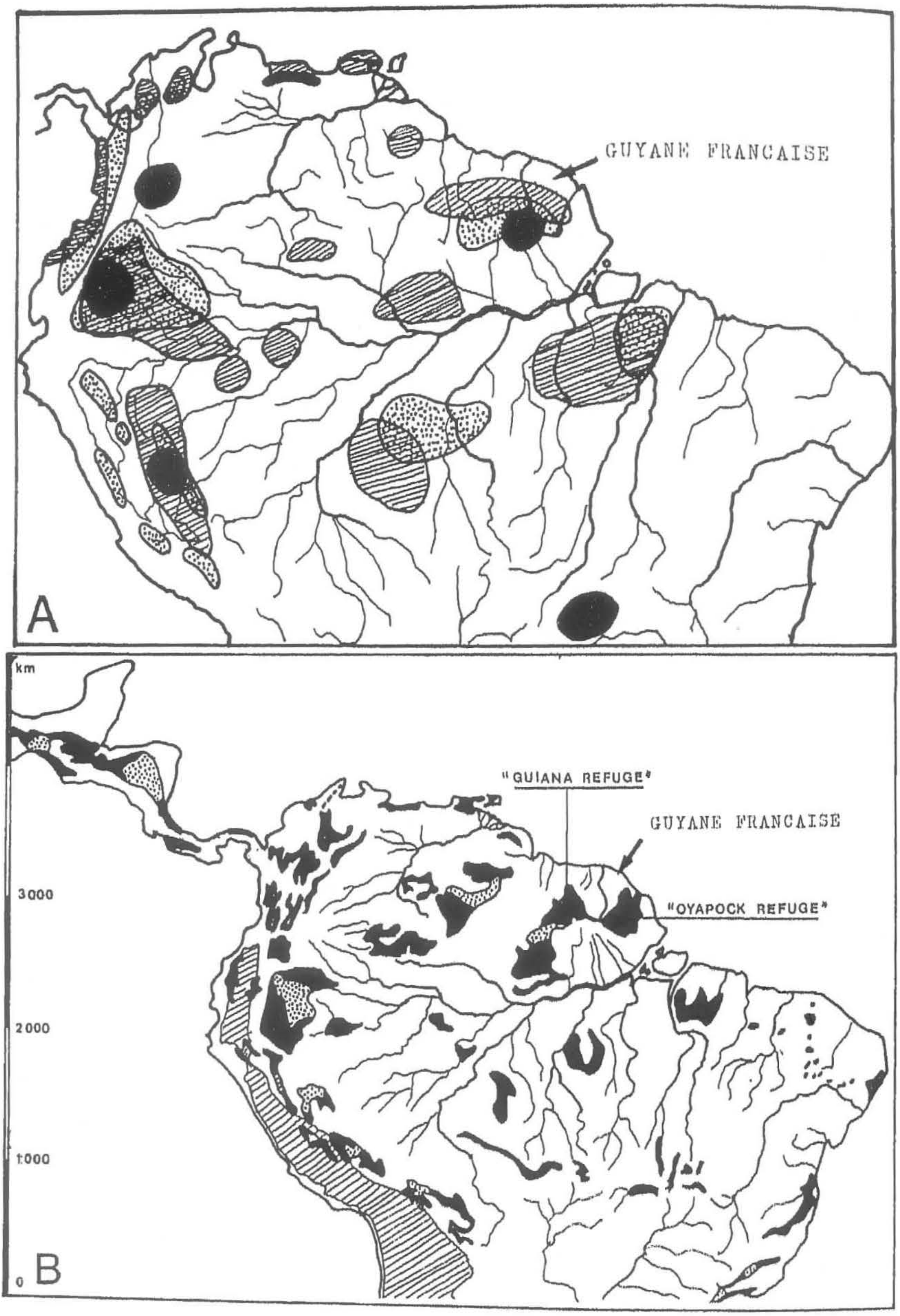
The rain forest which grows on well-drained clayey soils is only very locally replaced by other vegetation types or communities, i.e., swamp forest or "pinotières" ("Igapó forest" in Brazil) along certain water courses; "cambrouses" or thickets of bamboos; rocky savannas on denuded granite outcrops; low lying scrub forest on the lateritic crust of the summits of the plateaus; and cloud forest rich in epiphytes covering the summits above 500 m (although relatively hilly French Guiana doesn't have any very high peaks (fig. 12.4).

The forest flora is rich. Botanists from the Office de la Recherche Scientifique et Technique Outre Mer (ORSTOM), after more than twenty years of research and exploration in French Guiana, reckon the number of vascular species to be between 6,000 and 8,000. A precise inventory is in the process of being made, but there is still no specific flora which provides easy identification of species. Up to the present, research has dealt mainly with the collection of herbarium specimens, the phytoecology of the savannas, the dynamics, ecology, and architecture of the forest, and regeneration of the vegetation after cutting and burning.

Late Quaternary Climatic Fluctuations and Probable Evolution of the Flora

Paleoclimatic research undertaken by numerous disciplines (geology, geomorphology, palynology, biogeography), and studies of solar radiation and analysis of the isotopic composition $^{18}O/^{16}O$ of marine sediments, have permitted the establishment with remarkable precision of the climatic variations on earth during the Quaternary. (Among the very many authors who have approached this subject we can mention: Ab' Sáber, Absy, Bigarella, de Boer, Damuth and Fairbridge, Gates, Imbric and Kipp, Journaux, Lamb, Lorius and Duplessy, Maley, Meggers, Milankovitch, Müller, Tricart, Van Geel, Van der Hammen, Vanzolini, Vuilleumier, and Wijmstra.) We know in particular that the last of the six important Pleistocene glaciations, the Würm (70,000–10,000 B.P.) was marked by a succession of four glacial stages broken by interstadials. During the glacial stages part of the water in the oceans was immobilized in the polar icecaps, and the climate in general, including that of the intertropical regions, was colder and drier. During the interstadials, the warming up of the climate was accompanied by an increase in the rainfall and in the amount of water contained in the atmosphere at saturation point (Tricart 1974).

The last big glacial episode of the Würm, occurring between 22,000 and 13,000 B.P., is the one which has particularly interested scientists because of the importance of its biogeographical consequences. The drying up of the climate gave rise to an important retreat of the forest which, notably in South America, was situated at this time in a certain number of refuges, where the local climatic conditions favored its mainte-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nance. These refuges acted as centers of preservation and diversification. On the other hand, during the interglacial periods the coalescence of the forest gave rise to the contact and hybridization of species and subspecies which were genetically isolated. Although the number and area of the refuges proposed by different authors may differ (fig. 12.5), it is a fact that their distribution on the periphery of the Amazon basin is on the whole the same in all cases and that in each case there exists a Guianian refuge which is partially situated in French Guiana.

Other dry episodes which have been much shorter and less intense have marked the Holocene, especially between 11,000 and 9,500 B.P. (Dryas recent or "El Abra"), and between 3,500 and 2,800 B.P. According to Brown (1977) they did not last long enough to give rise to an important fragmentation of the flora. Zonneveld (1975) estimates, however, that between 5,000 and 2,400 B.P. the American rainforest was largely replaced by savanna, and Journaux (1975:32) suggests that the "Savannes 'incluses' fréquentes au nord de l'Amazone sont des témoins peut-être attardés de la dernière phase sèche ou d'une ultime oscillation climatique se situant alors vers 4000–2000 ans B.P." I also think that these recent dry periods during the Holocene, without causing the break-up of the forest during the Pleistocene, did exert a certain impact on the vegetation by delaying the advancement of the forest and also by inducing small local savannizations and the uncovering of granitic outcrops.

It suffices to say that each dry period did not necessarily affect the tropical regions in the same way. Brown (1977) noted that the distribution of the forest refuges has been very different during each climatic cycle. It is probable that during the short dry periods of the Holocene the maximum rainfall was not geographically the same as that during the end of the Pleistocene. Both Zonneveld (1975) in Surinam and Journaux (1975) in his geomorphological study of Brazilian Amazonia showed that the phenomenon of "climatic pulsations" must be considered along with the phenomenon of displacement of climatic zones in space: "Les savanes du Roraima et du pays des Tirios se sont étendues aux dépens de la forêt; cette conquête s'est effectuée du Nord au Sud dans le pays des Tirios" (Journaux 1975:28).

French Guiana in the Context of Climatic Fluctuations

In what follows, we intend to analyze briefly the information we have obtained on the natural environment of French Guiana that may give us some general indication of the existence, location, and extent of the forest refuges during the glacial periods and of the low-lying xeric vegetation refuges during the interglacial periods.

Rain Forest Refuges during the Arid Periods

We will limit ourselves to the period from 22,000 B.P. up to the present.

Figure 12.5 Rain forest refuges in tropical America during the late Pleistocene (22,000–13,000 B.P.).

A. ■ according to Vanzolini (1970, 1973).
▨ according to Prance (1973).
░ according to Haffer (1969).

B. according to Brown (1977).

Biogeography alone cannot provide information complete enough to construct a refuge model. At present, the establishment of an area of distribution of certain plant species on a relatively precise map is unlikely. In fact the floristic data collected on explorations are much too fragmentary for three reasons: certain regions are still little or not at all explored; others have been explored only during a single season of the year so that the species flowering or fruiting during the other seasons have not been collected; and although a special effort has been made towards the identification of herbarium specimens in recent years the task is still unfinished, especially where it concerns species that are rare, have a small distribution, or are new or endemic.

Nevertheless, in considering the information as a whole, even though fragmentary, on the natural environment of French Guiana which has been provided by different areas of study, it is possible to draw up an approximate map of the zones which have been probable forest refuges during the most recent dry periods.

The geographic distribution of rainfall during the dry periods of the past cannot in general be extrapolated from data concerning present-day climatic conditions (Tricart 1974; Zonneveld 1975). However, there are regions in French Guiana where, because of the topography, the rainfall remained continually abundant. These are found where mountain massifs are large and high enough for the existence of microclimates which are very humid because of convection currents and dew. The mountains of this type in French Guiana are mostly situated along the "Inini-Camopi range" (figs. 12.2, 12.4), on table summits of 500 to 900 m altitude covered with a thick lateritic or bauxitic crust. They witnessed dry and humid episodes long before the Würm; the most recent crust of this category dates from the Eocene (Boulet, pers. comm.). It is the "first peneplain" of Choubert (1957) and corresponds in Surinam to the "Kopinang surface" of which the Nassau mountains form a part (McConnel 1966; de Boer 1972). These crusts at relatively high altitudes have therefore no connection in their formation with the events of the late Pleistocene. The forest which covers them is very hygrophilic in spite of a scrubby aspect due to the mechanical difficulties in rooting encountered by the big trees.

The pedological map of French Guiana (fig. 12.6), closely linked to the physiognomy of the vegetation, provides only a few indices that can identify those soils which stayed under forest during the recent arid phases and on those which indicate the presence of savanna.

From among the possible forest refuges, one can eliminate the following zones:

1. The lowland soils of the recent coastal plain (fig. 12.6: 1–3), saline, silty, hydromorphic, flooded during the Flandrian trangression, corresponding to the climatic optimum of the present interglacial which occurred around 6,000 B.P., and which, today, are covered at high tide. They are covered with mangroves and subcoastal marshes. These sediments were laid down in the course of three stages (Mara—2,700 B.P.; Moleson—1,600–1,000 B.P., Comowine—800–0 B.P.).

2. The soils of the former coastal plain (fig. 12.6: 4), composed of more or less sandy leached clays, sometimes hydromorphic, of which the summit does not exceed the ordinance datum level + 5 m. They also were covered 6,000 years ago by the sea to a level about 10 m above today's mean. (10 to 50 m according to Charlesworth and Emiliani in Vuilleumier-1971—, 5 to 12 m according to Ab'Sáber in Brown [1977]). Today, these soils are covered either with dry coastal savannas or swamp forests rich in palms, therefore belonging to recent implantations and having a fragile equilibrium (de Granville 1978). "In South America, following the establishment of herbaceous swamps, palms appear to enter as "initial stages" in the formation of seasonal swamp forest or of true swamp forest" (Moore 1973:65).

3. The precoastal sandbars, sometimes rising above the clays of the former coastal plain (maximum altitude : + 13 m),

which were also partially submerged 6,000 years ago and which today are covered by savanna and forest with xeric tendencies.

4. The leached, hydromorphic soils of river alluvia (fig. 12.6:13), at present occupied by swamp scrub forest, probably flooded 6,000 years ago and made up at that time of little interior lakes.

5. The podzols of the "*série détritique de base*" (fig. 12.6:5), situated in the St. Laurent region (white sand forests).

It is unlikely that, among the upland soils, which today are completely covered with forest, the following categories have remained permanently forested during the last 20,000 years:

1. The continental sandy-clayey eluvia which are leached or hydromorphic, badly drained (fig. 12.6:12), and which support a scrub forest of mediocre physiognomy and with a rather poor flora.

2. All soils in which there is a compact B horizon more or less impermeable, having a lateral drainage with a lot of superficial water, and which favor savannization (Humbel, pers. comm.). These soils, according to Boulet (pers. comm.), are found principally on the migmatites.

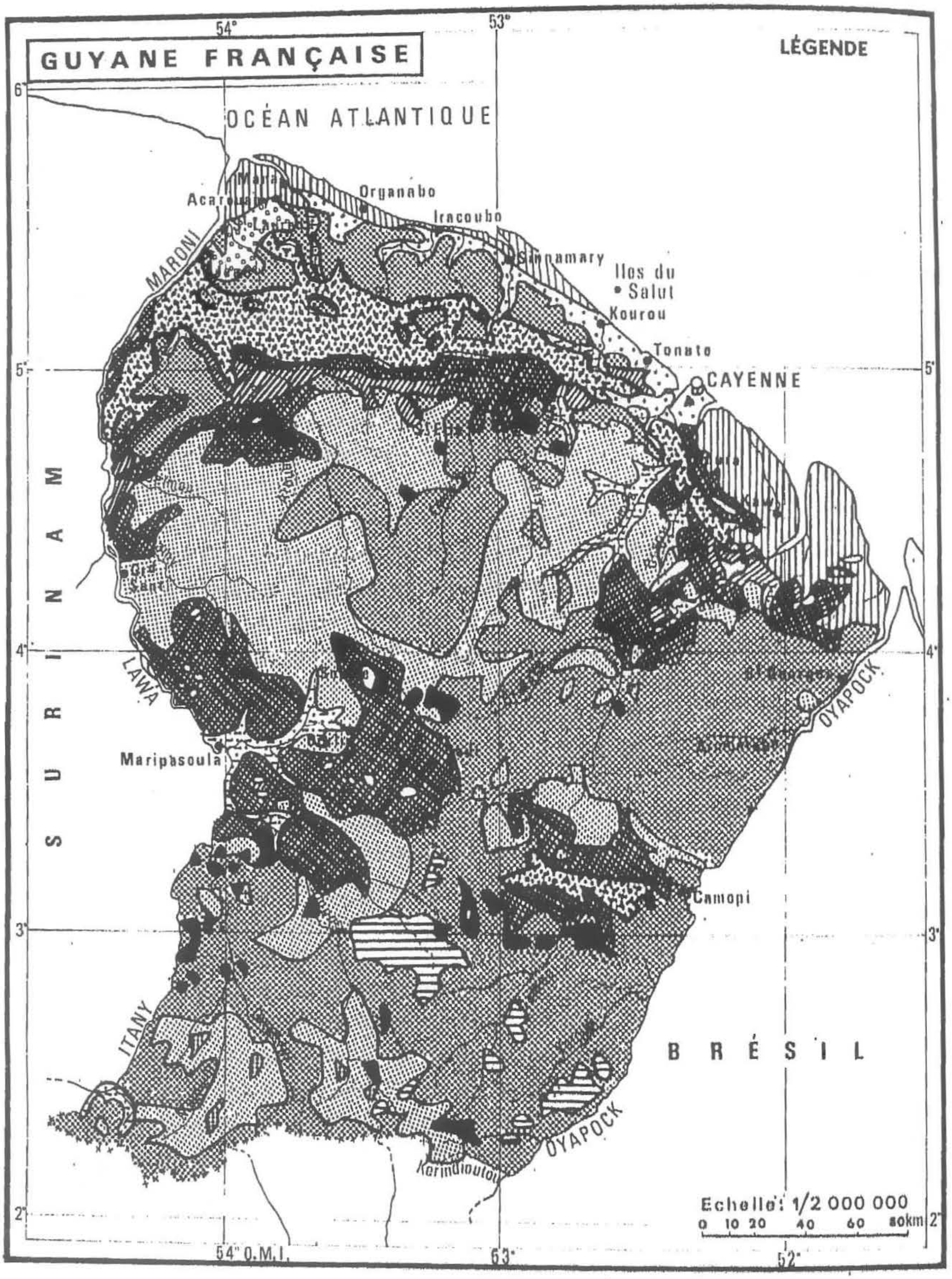
On the other hand, one is led to believe that the upland soils with free vertical drainage (i.e., in which the B horizon is not impermeable), are characteristic of the zones which favor the maintenance of the forest during dry climatic periods. At present, the "finest" forests are found growing on these deep, chemically rich, and well-drained soils. These forests contain tall trees with hard wood that are witnesses of advanced sylvigenetic phases (Budowski 1963, 1965). It seems that such soils, associated with a highly stable forest, rich in species, predominate in the interior of French Guiana, principally in the central region (the Saül region is a very good example). These soils are found on moderate slopes of either granite (multiconvex relief in "demi-oranges" of "granites guyanais") or schist and also even on steep slopes whose rock type is basic. The basic lavas of the "paramaca" series (fig. 12.6:10), called "roches vertes," seem to be the most favorable for the maintenance of "fine" forests. According to Boulet (pers. comm.), the crystalline rocks of certain northern plateaus, as well as those of the southern peneplain are covered by soils with moderate vertical drainage and therefore one cannot affirm that they have always been completely wooded.

The pedological map of French Guiana does not show the existence of "stone lines", conglomerates, etc., that could provide evidence of former deforestations (Ab'Sáber, Journaux, in Brown 1977).

The pedological information must be used with much caution and reserve because the paleoclimatic influences have not been tested with precision and have moreover in large part been obliterated by tectonic movements (Boulet, pers. comm.): the gentle uplifting of French Guiana induced a complete transformation of the ferralitic soil cover. It is these intermittent epeirogenic movements (Choubert 1957; McConnel 1966; Van der Hammen 1969; de Boer 1972) which gave rise to various peneplains which have been successively eroded and reconstructed.

The tectonic movements have had a greater influence on the geomorphology of French Guiana than the recent climatic variations. This is why one cannot expect too much information on the recent paleoclimatology from the geomorphological map (*Atlas de la Guyane* 1979). However, Zonneveld (1975), in his geomorphological study of southern Surinam (Sipaliwini region), reckons that the fossil forms of erosion are proof of a savannization which dates from a few thousand years ago. The region studied by Zonneveld is adjacent to the southwest of French Guiana, which must have been affected by the recent savannizations. This is a region which falls within the annual isohyet of 2,000 mm, below which the growth of dense rain forest is precarious.

The relative richness and the affinities of the flora, which have been estimated very roughly, are represented on the map of figure 12.7. This must be considered as a working hypothesis only.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In keeping with the topographical and pedological information mentioned above, certain regions have floristic characteristics which do not argue in favor of a continuous forest refuge since the end of the Pleistocene. These are: the existing savannicolous flora of lowlands, the relatively poor flora of the southern peneplain and of the flat zones covered with continental eluvia, the savannicolous species in the white sand forests in northwest French Guiana also found in the "savanna bushes" of Surinam (*Clusia fockeana* Miq.—Clusiaceae; *Humiria balsamifera* St. Hil.—Humiriaceae; *Matayba opaca* Radlk.—Sapindaceae; *Myrcia sylvatica* Dec.—Myrtaceae) according to Van Donselaar (1965).

Even though nowhere in French Guiana is there a high number of endemics, it seems, according to our observations, that the region which is most rich floristically, which has the greatest number of endemic species, and which must have been part of the Guianian forest refuge, corresponds roughly to the zones with the greatest rainfall (fig. 12.7 : zone IIb) and to the mountains in the Inini-Camopi range (fig. 12.7 : zone III). The Saül region, where we have

Figure 12.6 The soils of French Guiana. According to J.-C. Blancaneaux, in *Atlas de la Guyane*, 1979.

Lowlands

1-3 ▥ *Soils of the recent coastal plain* (mineral and unevolved nonclimatic soils) on marine alluvia and sandy silt.

4 ░ *Soils of the former coastal plain* (ferralitic leached and/or impoverished soils, podzols, hydromorphic soils) on former sandbars and marine alluvia.

Highlands

5 ▦ *Soils of the "série détritique de base"* (ferralitic soils, highly desaturated in B, leached and/or impoverished, podzols) on white sands and yellow sands.

Ferralitic soils, highly desaturated in B, on Precambrian base

6 ▩ Characteristic reworked, rejuvenated, impoverished soils on "*schistes de l'Orapu*" (schist, conglomerate, quartzite).

7 ▨ Characteristic crusted, rejuvenated, impoverished soils on "*schistes de Bonidoro*" (schist, conglomerate, quartzite).

8 ░ Characteristic reworked, impoverished, rejuvenated soils on "*granites guyanais*" (granites, granodiorites, migmatites).

9 ░ Characteristic soils, reworked, rejuvenated, leached and/or impoverished in clay, on "*granites Caraïbe et Galibi*" (granite, granitogneiss, gneiss, migmatites, feldspar).

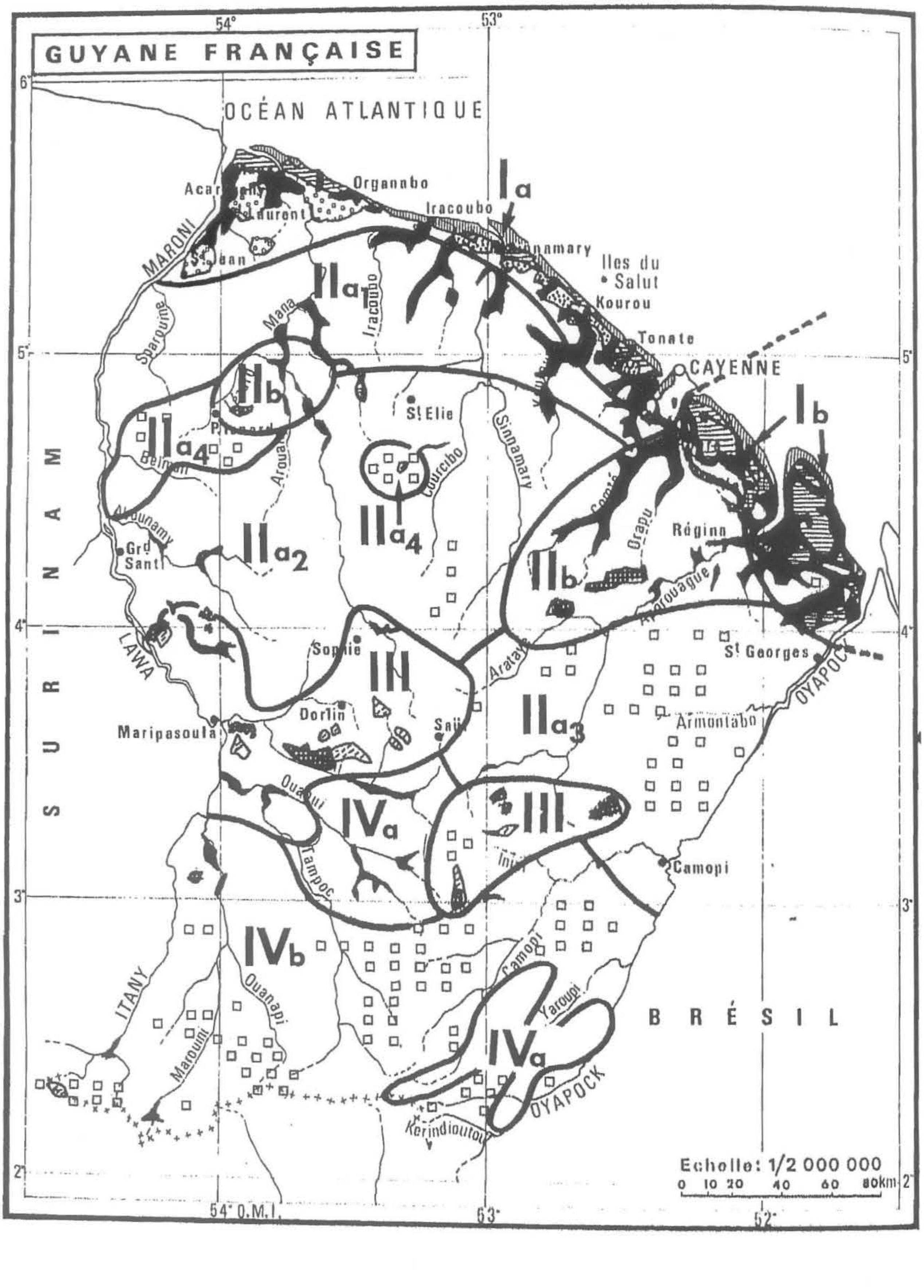
10 ▩ Characteristic reworked, rejuvenated soils on "*roches vertes de la série de Paramaca*" (schist, basic lavas, rhyolithes, tufs).

11 ■ Characteristic reworked, rejuvenated soils on *igneous rocks associated to "Paramaca"* (gabbros, peridotites, pyroxenolites, amphibolites).

12 ░ Characteristic leached and/or impoverished soils, hydromorphic soils, on sandy-clayey *continental eluvia*

13 ░ Characteristic leached and/or impoverished soils, hydromorphic soils on *fluviatile alluvia* (valley floors).

14 □ *Lateritic crusts.*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carried out regular collections of herbarium specimens during the past several years, has revealed a certain number of new species which are presumed to be endemics (fig. 12.8). These are, for example, *Episcia xantha* Lwb. (Gesneriaceae), *Elephantomene eburnea* Barneby & Krukoff (Menispermaceae)—new genus—, as well as four undescribed *Psychotria* species (Rubiaceae), in particular : *P. granvillei* Steyermark exclusively localized on the La Fumée mountains, 5 km north of Saül, which is sympatric with *P. poeppigiana* Mull. Arg., a species distributed all over tropical America; and *P.*

Figure 12.7 Flora and vegetation

▥ Mangrove
░ Herbaceous swamps
░ "Dry" savannas
░ White sand forest
■ Marsh forest and swamp forest
▥ Forest on lateritic crusts
□ Rain forest on well-drained ferralitic soils (alt. 500m)
░ Cloud forest (alt. 500m)
⁝ Zone rich in rocky slopes and outcrops

I. COASTAL SECTION: Lowlands, on marine alluvia (mangrove, savannas, swamps and marshes, coastal forests, and transitional zones).

Ia. *Lowland zones which have a tendancy to be dry, west of Cayenne.*

Vegetation: mangrove, savannas, secondary vegetation and cultivation, forests on sand with some xeric tendancies.

Flora: very varied, particularly with Surinamian affinities; pantropical species frequent.

Ib. *Humid zones in the lowlands, east of Cayenne.*

Vegetation: mangrove, large marshes, swamp forests, "pinotières."

Flora: varied, with Amazonian affinities.

II. MEDIAN AND SUBCOASTAL SECTION: Northern Range and Central Massif (forest).

IIa. *Zone with mean rainfall.*

Vegetation: dense rain forest, more or less "fine."

Flora: fairly species-rich; varied affinities.

IIa1. Subcoastal forests on "Orapu" schists, generally "fine" and species-rich; Guianian-Surinamian floristic affinities.

IIa2. Forests on the western median zone on crystalline base, "fine" to mediocre, fairly species-rich; varied floristic affinities, mainly Surinamian.

IIa3. Forests of the eastern median zone on crystalline base, "fine" to mediocre, fairly species-rich; varied floristic affinities, mainly Amazonian.

IIa4. Forests of submountainous zones on uneven bases, generally very "fine" and species-rich; floristic affinities very varied, sometimes mountainous.

IIb. *Zones with very high rainfall* on varied bases and transitional zones. Extensive lateritic crusts of low altitude.

Vegetation: Dense rain forest, generally very "fine."

Flora: very rich due to the rainfall and the variety of habitats; very diverse floristic affinities.

III. ININI-CAMOPI RANGE SECTION (forest), mostly on *roches vertes*. Zone of the extensive altitudinal crusts; habitats varied and contrasting; soils generally deep.

Vegetation: dense rain forest, generally very "fine" and majestic: submountainous scrubby forest on lateritic crusts.

Flora: very rich, bearing endemic hygrophile species on the summits; very diverse affinities, often Surinamian and and mountainous.

IV. MERIDIONAL SECTION: Southern Peneplain (forest).

IVa. *"Flats" zones and extensive eluvial plains.*

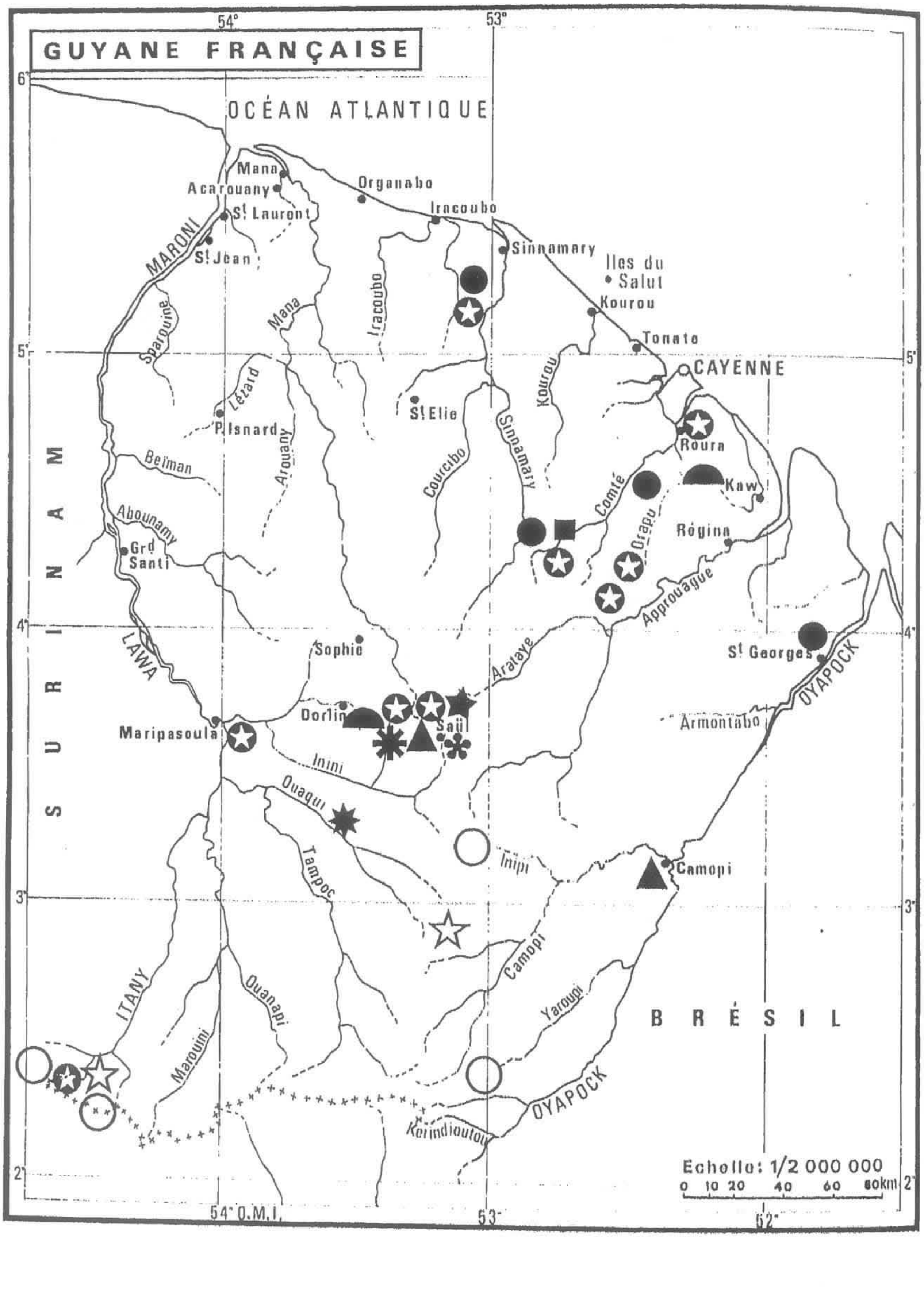
Vegetation: dense rain forest, often mediocre and scrubby.

Flora: generally poor.

IVb. *Hills and outcrops zone on crystalline base.*

Vegetation: dense rain forest, more or less "fine"; mesophilic forest, bush and xeric herbaceous vegetation on the rock slopes and outcrops.

Flora: fairly poor, becoming rich in the higher irregular zones and on the outcrops. Presence of endemic species on the latter. Very diverse floristic affinities (especially Amazonian for the forest species and coastal or mountainous for outcrop species).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galbaoensis Steyermark which grows on the Galbao mountains (alt. : 600 m approx.), 10 km west of Saül, but not sympatric with *P. urniformis* Steyerm. which is endemic to the Ayanganna mountains in Guyana (ex British Guiana), at an altitude of 800 m. These two highland species are probably the result of isolation on mountains which remained wooded during the dry phases in Guyana and French Guiana. Among recently described endemic species of French Guiana we note *Anomopaegma granvillei* Gentry (Bignoniaceae), on the Ouaqui river, and *Geonoma oldemanii* J.-J. de Granville (Arecaceae) which is found in the swamp forests around St. Georges, on the upper Sinnamary river and to the north of St. Elie. This last species is taxonomically closest to *G. chococola* W. Boer (de Granville 1975).

It would be of great interest to study in other neotropical refuges the species resembling these endemics which have been genetically individualized following their isolation. The counting of the chromosome number in the study of hybrids would also help in determining the regions where forest floras have come into contact with each other at the time of recoalescence of the forest.

Other species found in the primary forest in Saül occur also in regions far distant from French Guiana. These areas, which are very disjointed, could provide evidence of isolation, both in the Guianas and elsewhere, of species that have not evolved during this isolation to the degree that the beginnings of speciations are discernable. These species are:

Adiantum cordatum (Adiantaceae): Saül + Panama (Brown's Chiriqui or Darién refuge, 1977); *Anomospermum chloranthum* subsp. *confusum* (Menispermaceae) : Saül + Peru—Huánuco, Loreto (Napo refuge); *Oedematopus octandrus* (Guttiferae) : Saül + Rio Negro (Manaus refuge). However, just because of these few forest species that have a disjointed distribution, one cannot completely eliminate the hypothesis (although an unlikely one given that these species grow in primary forest) of a recent dispersal by man, nor ignore the fact that insufficient botanical exploration in Amazonia may have failed as yet to establish the presence of these species in intervening localities.

←

Figure 12.8 Distribution of Some Species Endemic in French Guiana

I. Rain Forest, Humid Flora

Vascular plants

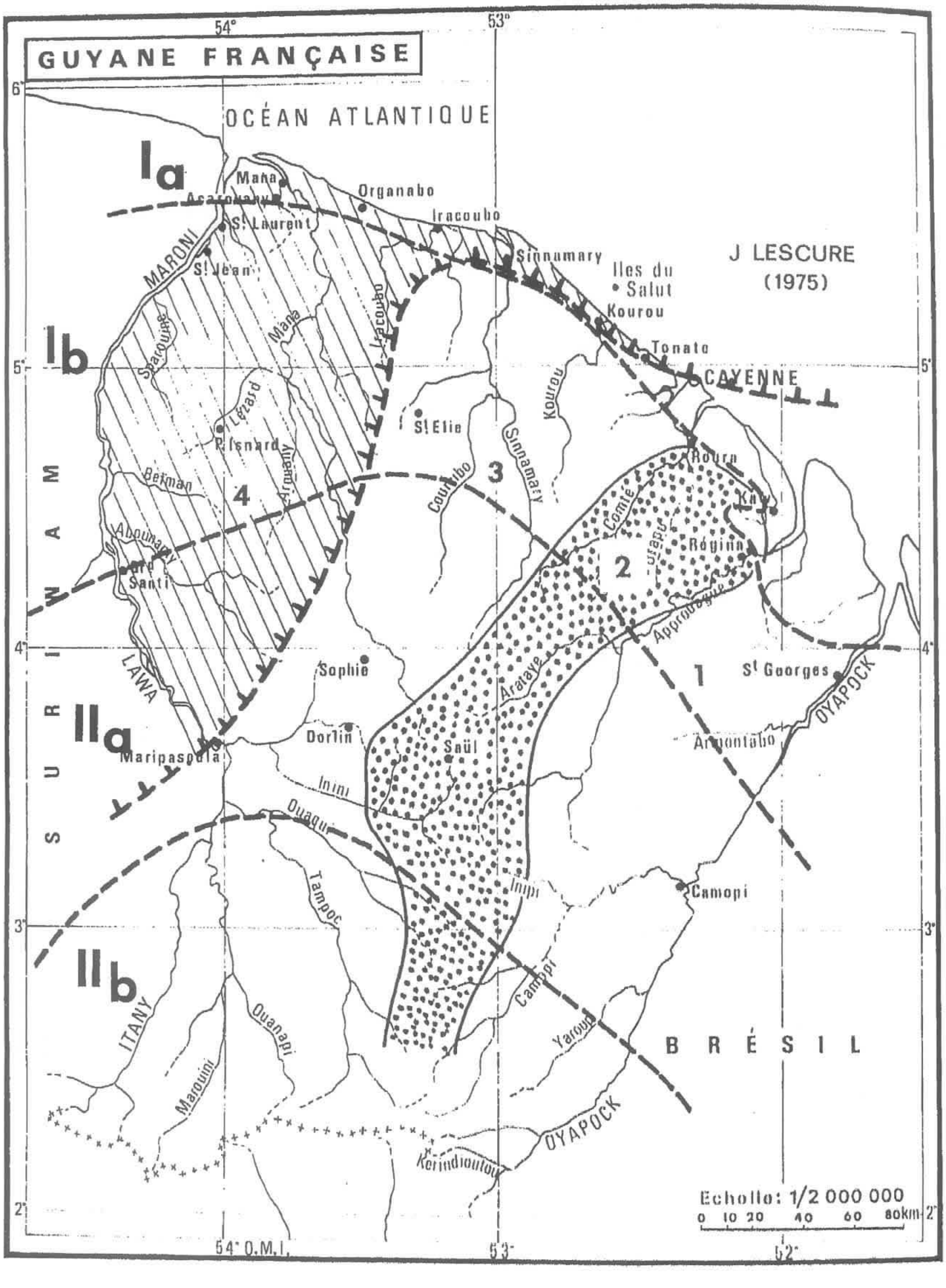
❋ *Anomopaegma granvillei* (Bignoniaceae)
★ *Elephantomene eburnea* (Menispermaceae)
◓ *Episcia* sp. nov. (Gesneriaceae)
● *Geonoma oldemanii* (Arecaceae)
▲ *Heliconia lourteigii* (Musaceae) also found in Peru
■ *Palmorchis prospectorum* (Orchidaceae)
❋ *Psychotria* sp. nov. aff. *urnifera* (Rubiaceae)
✱ *Psychotria* sp. nov. aff. *poeppigiana* (Rubiaceae)

Amphibian

✪ *Colostethus degranvillei* (Dendrobatidae)

II. Outcrops, Xeric Flora

○ *Pitcairnia geyskesii* (Bromeliaceae)
☆ *Pitcairnia sastrei* (Bromeliaceae)


GUYANE FRANÇAISE
54°
53°
6°
5°
4°
3°
2°
OCÉAN ATLANTIQUE
Ia
Ib
IIa
IIb
1
2
3
4
Mana
Acarouany
St Laurent
Organabo
Iracoubo
Sinnamary
Iles du Salut
Kourou
Tonate
CAYENNE
J LESCURE
(1975)
MARONI
St Jean
Sparouine
Mana
Iracoubo
Lézard
P. Isnard
St Elie
Sinnamary
Kourou
Beïman
Argenty
Courcibo
Comté
Roura
Orapu
Kaw
Régina
Abounamy
Grd Santi
S U R I N A M
LAWA
Sophie
Arataye
Approuague
St Georges
OYAPOCK
Maripasoula
Dorlin
Saül
Inini
Arpontabo
Ouaqui
Tampoc
Inini
Camopi
ITANY
Ouanapi
Marouini
Camopi
Yaroupi
B R É S I L
OYAPOCK
Kerindioutou
Echelle: 1/2 000 000
0 10 20 40 60 80km
54° O.M.I.
53°
52°

As far as we know, no palynological research has been undertaken in French Guiana.

Within the domain of zoology, the batrachologist Lescure (1975:81), studying the biogeography of the amphibians in French Guiana, concluded that there probably existed "... un centre de spéciation qui, dans sa partie de Guyane Française, était situé au nord du Tumuc-Humac, entre le Tampoc et le Camopi, autour de Saül, et entre la Comté et l'Approuague" (fig. 12.9). *Colosthetus degranvillei* (Dendrobatidae) is a characteristic example of a species endemic to French Guiana whose area of distribution corresponds to that of the proposed refuge. Lescure relates this species, from the taxonomic point of view, with *C. infraguttatus* (Andes south of Ecuador), *C. inguinalis* (Colombia and notably in the Chocó refuge) and especially with *C. bocagei* (Ecuador). It seems therefore that there are species resulting from isolation in the north Andean refuges and in the French part of the Guianian refuge.

By the way of conclusion, we propose, with fair certainty, the existence of a forest refuge between 22,000 and 13,000 B.P. which occupied the central and eastern zone of French Guiana, limited to the north by the Kaw mountain and to the south by the Inini-Camopi mountain range (fig. 12.10) (cf. arguments concerning the climate, topography, pedology, botany and zoology which have been outlined in the text). The eastern and western limits of this refuge are still not well defined. To the west, the refuge reached the Maroni river at the level of the Atachi Bacca mountains, but it is possible that it also covered the multiconvex crystalline base to the north of the Inini-Camopi mountain range, near the 5° parallel. To the east, it is quite likely that this refuge reached Brazil beyond the Oyapock, between St. Georges and Camopi. On the other hand, it is not absolutely certain that either the northern mountain range, on schist, conglomerate, and quartzite ("Bonidoro" series), or the southern peneplain rich in outcrops were part of this continuous forest refuge.

To be excluded are the coastal lowlands, the alluvium and eluvium zones of the interior, the podzols of the St. Laurent region at the extreme NW, as well as the SW region where traces of deforestation are still visible in the relief and in the vegetation (Hurault 1973; de Granville 1978).

Furthermore, we reckon that, just as the rainfall gradient of the isohyets in space exists, the limits of the refuge between forest and savanna cannot be precisely defined in a linear fashion, except in the north where it abuts against the alluvial coastal plain between Cayenne and St. Georges. As one moves further away from the zone covered

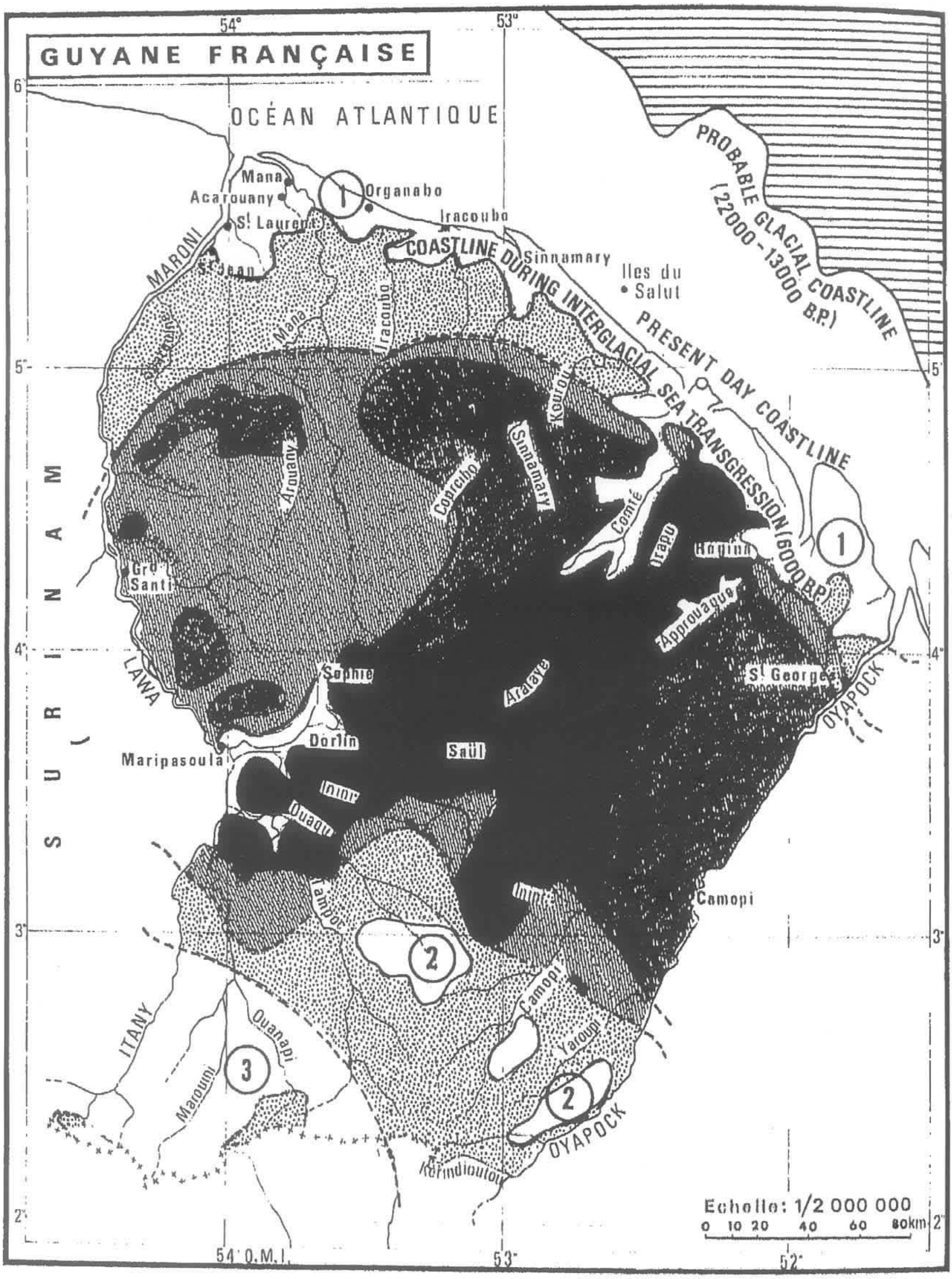
Figure 12.9 Climatic and Biogeographic Regions in French Guiana. According to J. Lescure (1975).

— — — — Climatic zones

- I. Coastal region
  - Ia. Coastal zone
  - Ib. Middle zone
    - 1. Eastern group
    - 2. Roura group
    - 3. Cayenne group
    - 4. Western group
- II. Interior region
  - IIa. Southern zone
  - IIb. Extreme southern zone

▨ Zone with Surinamian affinities

░ Forest refuge


GUYANE FRANÇAISE
OCÉAN ATLANTIQUE
54°
53°
6°
5°
4°
3°
2°
Mana
Acarouany
Organabo
1
St Laurent
Iracoubo
St Jean
MARONI
COASTLINE DURING INTERGLACIAL SEA TRANSGRESSION (6000 B.P.)
PROBABLE GLACIAL COASTLINE (22000-13000 B.P.)
PRESENT DAY COASTLINE
Sinnamary
Iles du Salut
Mana
Iracoubo
Kourou
Sinnamary
Arouany
Coneibo
Comté
Orapu
Approuague
1
SURINAM
Gr Santi
LAWA
Sophie
Dorlin
Saül
Arataye
St Georges
OYAPOCK
Maripasoula
Inini
Ouaqui
Tampoc
Inini
Camopi
2
Camopi
Yaroupi
ITANY
Ouanapi
3
Marouini
2
OYAPOCK
Koerindioutou
Echelle: 1/2 000 000
0 10 20 40 60 80km
54° O.M.I.
53°
52°

with continuous forest in order to reach the savannas and the dry forests which encroach progressively on the dense rain forest, one must cross vast transition regions of a forest-savanna mosaic, where the forest takes refuge along the water courses (gallery forests) and hill slopes exposed to the trade winds. Such was probably the case in the southern peneplain and, in general, in the zones adjacent to the continuous forest refuge.

The geomorphology of French Guiana does not seem to indicate the presence in the past of vast regions completely covered with savannas. Also we reckon that the greater part of French Guiana remained covered, even if only partially, with forest during the last big glacial period at the end of the Pleistocene.

The more recent dry periods (11,000–9,500 B.P., less intense and much shorter as well as higher cannot have affected any large part of the vegetation cover in French Guiana. It suffices to recall, however, that the regions deforested during the most recent dry periods do not necessarily correspond exactly with those that existed during the arid periods at the end of the Pleistocene. Because of the high number of outcrops in the south and the way in which the vegetation evolves to recover the bare rocks in spite of an annual rainfall of less than 2,000 mm, it would seem that the most recent dry episode has mainly affected the extreme south of French Guiana.

> Dans le Sud de la Guyane Française et, plus spécialement dans le Massif du Mitaraka, on observe sur les crêtes des boules de granite tandis que d'autres ont roulé le long des versants et se sont accumulées dans le fond des thalwegs. Leurs formes sont remarquablement fraiches : il est permis d'y voir les preuves d'une phase climatique sèche très récente (quelques milliers d'années, peut-être quelques siècles) ayant entrainé la destruction de la forêt. Celle-ci est actuellement en nette progression, témoignant d'un accroissment de la pluviosité (Hurault 1973:53)

This confirms what we said above, following the research of Zonneveld (1975) in Surinam, and agrees with the study which we carried out in the Tumuc-Humac region (de Granville 1978). We think that the zone with a drier climate above the relic savannas in the Tirios country (to the south of Surinam) has recently touched upon the southwest of French Guiana in the course of its displacement towards the south (Journaux 1975).

Figure 12.10 Presumed rain forest refuges of French Guiana—22,000–13,000 B.P.

■ Very high probability continuous refuge zone.

▦ High probability continuous refuge zone.

▥ Average probability continuous refuge zone (or very high probability mosaic and network refuge zone).

⬚ Low probability continuous refuge zone (or high probability mosaic and network refuge zone).

□ Very low probability continuous refuge zone (or average probability mosaic and network refuge zone):

1. Coastal zone, flooded in 6,000 B.P.
2. Continental alluvia
3. Zone which could have been part of a continuous forest refuge during the Pleistocene but probably savannized in the Holocene (3,300–2,800 B.P.).

Arid Flora Refuges During the Wet Periods

The present situation corresponds to the end of a warm and humid interglacial period. The study of the vegetation in French Guiana shows the presence of discrete isolated sites (with the exception of epiphytic communities in the canopy) which act as refuges for an essentially herbaceous and heliophilic xeric flora (fig. 12.11).

1. *The coastal savannas*. The "dry" savannas distributed along the coastline between Cayenne and Iracoubo are not the same as humid savannas or coastal swamps which are mainly situated to the east of French Guiana between Roura and the Oyapock delta.

The flora and phytoecology of the dry savannas, in which the Gramineae and Cyperaceae predominate, has been studied by Hoock (1971) in the Kourou region. This author distinguishes the "low savannas" growing on podzols with a low-lying very discontinuous xeric vegetation and a relatively poor flora, from the "high savannas" on ferralitic soils with a higher more continuous and less xeric vegetation and a somewhat richer flora.

The origin of these savannas is due to a number of interacting factors: edaphic, microclimatic (ventilation, dry season more accentuated than in the interior) human (presence of important Amerindian populations in the past; present annual fires). In addition, as we have already remarked, the savannas were submerged by the ocean ± 6,000 years ago, at the time of the interglacial climatic optimum. This considerably limits their role as a refuge, which cannot be continuous in time. This is why their flora, poor in endemics, is composed of elements with a generally vast area of distribution, that have undergone a selection of the "*r*" type.

Relic savannas comparable to those in southern Surinam and Venezuela do not exist in the interior of French Guiana.

2. *Outcrops ("Rock savannas") and emergent rocks in rivers*. The outcrops and emergent rocks in rivers both have a discontinuous xeric, saxicolous vegetation, and their floras are fairly similar. We have studied the vegetation of outcrops in the Tumuc-Humac region (SW French Guiana), where it is possible to recognize several distinct features of the vegetation depending on the slope, the drainage conditions and the aspect. The most xeric facies is made up of thick clusters of succulent orchids, the least xeric one, on slight slopes and thin soils, has a continuous vegetation with a much richer flora dominated by *Ischaemum guianense* Kunth (Gramineae). Between these two extremes, the facies with *Pitcairnia geyskesii* L. B. Smith (Bromeliaceae) occupies by preference the ridges and summits of the outcrops.

Analysis of the Tumuc-Humac flora shows that a certain number of vascular species are equally saxicolous and savannicolous, and can also grow on the coastal savannas (25% de Granville 1978; 40% Sastre 1976); for example, *Borreria latifolia* (Aubl.) K. Schum. (Rubiaceae); *Chelonanthus uliginosus* (Griseb.) Gilg (Gentianaceae); *Heliconia psittacorum* L.f. Musaceae); *Stylosanthes hispida* Rich. (Papilionaceae); and *Xyris fallax* Malme (Xyridaceae). These are the species that will partially contribute, during the next dry climatic phase, to the restocking of the territories lost by the forest.

Other strictly saxicolous species grow on outcrops as well as on the rocks of the rivers. Some of these, which only grow on the highest outcrops (greater than 500 m) on the Tumuc-Humac, show orophilic affinities, for they are absent from the plains but found on the summits, often much higher, in the south of the Guianas and in Venezuela. Such is the case for *Clusia kanukuana* Maguire (Clusiaceae), *Pitcairnia geyskesii* L. B. Smith (Bromeliaceae) and *Mandevilla surinamensis* (Pulle) Woodson (Apocynaceae), endemics of the Guianian outcrops

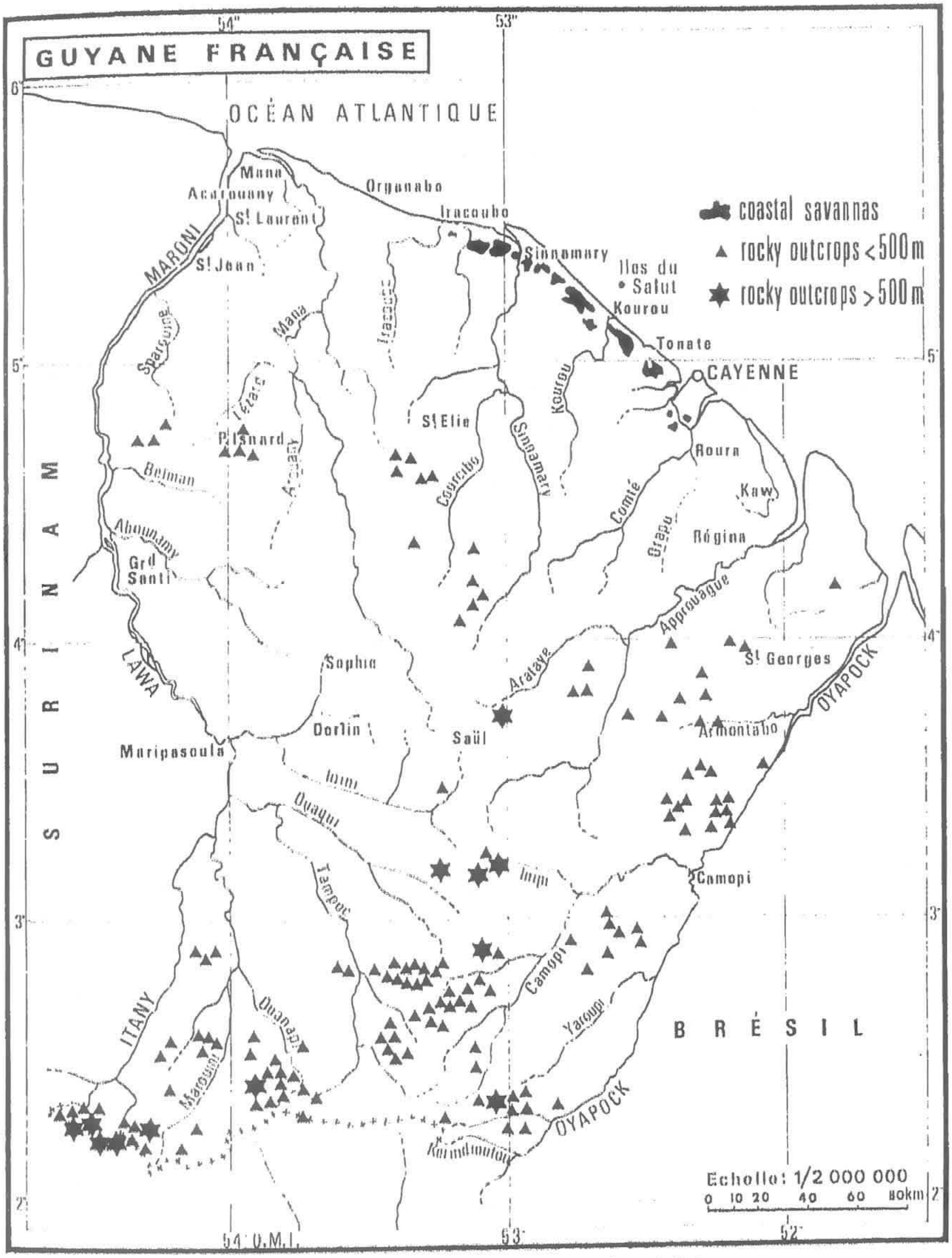


Figure 12.11 Present-day xeric refuges of French Guiana

between 500 and 1000 m. Some species are found both on the sandstone formations of Roraima (up to 3000 m) and on certain outcrops of Tumuc-Humac. These are *Clusia annularis* Maguire (Clusiaceae), *Sauvagesia tafelbergensis* Sastre (Ochnaceae), *Doryopteris sagittifolia* (Raddi) J. Smith (Cheilanthaceae). Most of these species reach on the Tumuc-Humac the lower limit of their present day altitudinal distribution. One must bear in mind the fact that, on an outcrop of 700 m during the arid phase at the end of the Pleistocene, where the altitudinal thermic gradient was more "compressed" (Van der Hammen 1974), the temperature was the same as that prevailing now on the summit of a 1,700 m mountain (de Granville 1978).

Xeric species, at the time of the warming up of the climate during the interglacial, must have adapted themselves to the higher temperatures in order to survive, or else must have taken refuge in sites where the mean temperature was lower than in the intertropical plain, that is to say at higher altitudes or latitudes or both at the same time. In this last case, the isolation has produced geographically disjointed species at a time when evolution was too slow to produce genetically distinct species: *Trilepis kanukuensis* Gilly (Cyperaceae), *Asplenium pediculariifolium* St. Hil. (Aspleniaceae), *Doryopteris sagittifolia* (Raddi) J. Smith (Cheilanthaceae)—found today on the rocky summits of the Guianas (on Tumuc-Humac and in Roraima) and in the region of Rio de Janeiro and southern Brazil. On the other hand, when the evolution was sufficiently rapid, the speciation which had been taking place since the moment of isolation produced related but distinct pairs of species such as *Rhynchospora subdicephala* Koyama (Cyperaceae), endemic on the outcrops of southern French Guiana and taxonomically close *R. lapensis* C. B. Clarke in Minas Gerais. All these species provide evidence of a former dry flora which was much more extensive.

Last, it is important to note that, like the forest refuges during the glacial periods, the xeric flora refuges during the warm humid interglacial periods (which are in particular the rocky outcrops) have also acted as centers of diversification.

3. The forest canopy. The forest canopy is a permanent dry flora refuge of which certain elements, both epiphytes and saxicoles, are able to contribute to the colonization of the rocky slopes and outcrops exposed to the sun and cleared by erosion during the recession period of the forest. Examples are *Aechmea setigera* Mart. (Bromeliaceae), *Epidendrum nocturnum* Jacq. (Orchidaceae), *Topobea parasitica* Aubl. (Melastomataceae). It is not surprising that such species have very extensive areas of distribution because they are not subjected to isolation of distinct populations in the course of climatic fluctuations.

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